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Review

Development Mechanism of Flower Type and Color in Tree Peony: A Review

Ding-Ding Zuo [1], **Da-Long Guo** [2,3,*], **Xiao-Gai Hou** [1,*]

[1] College of Agronomy/Tree Peony, Henan University of Science and Technology, Luoyang 471023, China

[2] College of Horticulture and Plant Protection, Henan University of Science and Technology, Luoyang 471023, China

[3] Henan Engineering Technology Research Center of Quality Regulation of Horticultural Plants, Luoyang 471023, China

* Correspondence: Da-Long Guo, E-mail: guodalong@haust.edu.cn; Xiao-Gai Hou, E-mail: hkdhxg@haust.edu.cn.

ABSTRACT

Tree peony originated in China and is world-renowned for its colorful flower. The flower type and color is one of the important ornamental characteristics of tree peony, and it is also an important reference index for peony cultivars identification and new cultivars cultivation. To date, tree peony has been divided into 10 flower types and 9 flower colors. The application of molecular technology has made a prominent contribution to the study of the regulation mechanism of peony flower development. Many functional genes and transcription factors that regulate flower color and type have been identified and applied to the study of peony. In-depth understanding of the regulation mechanism of flower type and color contributes to improving the ornamental value and breeding of tree peony. However, there is no systematic description of the regulation mechanism of flower type and color in tree peony. This review systematically described the research progress on the regulation mechanism of peony flower color and type, to provide reference for the research and breeding of peony flower development.

KEYWORDS: tree peony; flower; type; color

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INTRODUCTION

Tree peony (*Paeonia suffruticosa* Andrews) belongs to Paeoniaceae, and is famous for its large flowers, diverse colors, beautiful appearance and fragrance [1,2]. As one of the most popular ornamental plants in the world, tree peony is also a traditional medicinal plant in China [3]. And it has a long history of ornamental cultivation and more than 2000 varieties have been formed around the world after a long period of artificial selection and nature evolution [4,5]. The most major traits that change during long-term cultivation and domestication are the color and type of flowers,

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including the size and number of petals [6]. Different flower type and color are both valuable for the ornamental and potted production of tree peony, so they are pursued by breeders [7]. A better understanding of the molecular mechanism can provide a theoretical basis for breeding.

Flower color and type are one of the major biological traits of tree peony [8]. The understanding of the mechanism of flower color variation may contribute to the accurate classification of tree peony, which is the basis of peony breeding and genetic research. In recent years, many typical flower color regulatory genes have been identified based on multi-omics techniques, such as *PsCHS*, *PsCHI*, *PsDFR* and *PsANS* [8,9]. The flower color of tree peony has many phenotypic traits and the formation mechanisms are complex. Multiple basic substances involved in the formation of flower color, including flavonoids, anthocyanins and chlorophyll. And the color of the flower depends on the pigments accumulated in the petals and their respective concentrations [10–12]. However, the molecular regulation mechanism of flower coloration in many cultivars has not been described in detail.

As another significant ornamental characteristic of tree peony, the flower type can represent the evolution stage and status of each cultivar, reflecting the characteristics and natural evolution of the cultivars [13–15]. The evolution of flower type is restricted by environmental factors, especially the interference of artificial cultivation [4]. These studies focus on physiological changes and hormone analysis. To date, the flower development genetics of model plants have been systematically elucidated like Arabidopsis and Petunia [16]. Compared to the model plants, the understanding of flower development in tree peony is quite limited, especially the molecular regulation mechanism [13–15]. Stamen petalody leads to the increase of petals, resulting in different flower types, which is one of the most considerable characteristics of cultivar classification [17]. In tree peony, the wild species are basically single flowers, while the cultivated germplasm are different in the number of petals [8]. However, to date, the molecular mechanism leading to this difference is not clear. It is a valuable idea to try to reveal its internal mechanism by exploring the genes responsible for stamen or petal development. And flower type, as one of the major ornamental characteristics of peony, is also a significant reference index for cultivars identification and new cultivars cultivation [4,8]. Thus, it is of great significance to study the regulation mechanism of flower type for the personalized cultivation and breeding of tree peony.

Although the study of flower type and color have made great achievements in in tree peony [18]. However, compared with other plants, many of the regulatory mechanisms have not been described in detail, and there are still some gaps. And there is a lack of systematic summary of the regulation mechanism of flower color and type in tree peony. In this review, the research on the regulation of flower color and type in tree peony in recent years was reviewed in order to provide theoretical basis for the regulation of flower development in tree peony.

THE FLOWER RESOURCES OF TREE PEONY: COLOR AND TYPE

China, as the country with the most abundant peony resources in the world, has a long history of cultivation and is considered to be the most likely geographical origin of tree peony cultivation [4,5]. Some common tree peonies were introduced into Japan and Western countries, such as Britain and France, and developed into many distinctive varieties. To date, tree peony cultivars are generally divided into seven groups geographically. Among them, Zhongyuan cultivars, Xibei cultivars, Xinan cultivars, and Jiangnan cultivars belong to China, and there are three foreign cultivars, namely European cultivars, American cultivars and Japanese cultivars [19]. Generally, selective breeding and cross-breeding are the most common breeding methods [18]. The former focuses on selective breeding of seedlings and bud mutation, while the latter mainly includes two main types of cross-breeding: intrasubsectional and intersubsectional [3,18]. Although the traditional breeding method is very simple, but tree peony from sowing to flowering up to 3–5 years, and the offspring may be sterile, sowing and transplanting also requires a lot of land, some excellent individuals can only maintain variation by asexual reproduction [6,18]. Molecular breeding, chemical mutation breeding and radiation mutation breeding are supplements to traditional breeding methods. However, limited by tissue culture techniques, it is difficult to obtain a large number of seedlings through in vitro culture, resulting in the limitations of these methods. After long-term selective domestication, wild species have formed a variety of flower colors and types, which greatly expanded the germplasm resources of tree peony (Figure 1).

Flowers color, as a reproductive organ of tree peony, help to attract pollinators and facilitate the reproduction of the next generation [20]. For tree peony, flower color is a key factor to determine its ornamental quality, which directly affects its ornamental quality and commercial value. In addition, flower color is also one of the major biological traits and morphological indicators, which is often used as a basis for classification [18,21]. The flower colors of Paeonia are diverse, generally red, yellow, white or purple [21]. After a long period of artificial selection, peony has developed nine common color categories of native species, including green, yellow, pink, white, purple, red, blue, black and double color [21,22]. Among these colors, white is an excellent material for transgenic breeding with other color cultivars and red cultivars are in the majority, which are endowed with the meaning of festive and auspicious [23]. Tree peony with the same or similar flower color showed high genetic similarity and close relationship [23]. Flowers of different colors provide excellent candidates for exploring the basis of color molecular regulation of tree peony flowers.

Apart from flower color, the exploration of flower type regulation mechanism is also a research hotspot in tree peony. Flower type is another important ornamental feature of peony, and it is also the main basis for its classification [9]. To date, the flower type has been basically divided into ten types according to the number of petals and their morphological characteristics (the morphology, number, variation and arrangement of petals, stamens, pistils and sepals), including single-lobe type, lotus type, rose type, chrysanthemum type, globular type, crown type, anemone type, golden circle type, melaleuca proliferate-flower type and tower-like proliferate-flower type [24,25]. This is a comprehensive result of natural selection and plant evolution, especially artificial selection innovation. Among these flower types, the increase in the number of petals and stamen centripetal petals has resulted in a century of evolution from single-petal type to other flower types, including lotus type, chrysanthemum type and rose type. The differentiation of carpel primordium is a factor leading to the proliferation of flower type, which can be transformed and developed into various floral organs such as calyx and petal [25,26]. However, considering the complexity of flower type, the classification standard of flower type is constantly revised and supplemented with the progress of research. Various classification standards have basically the same understanding of the evolution law of flower type [24]. It is generally believed that the highest stable flower type (the number of flower types accounts for more than 60%) of a single cultivars is the typical flower type of the cultivars, while the atypical flower type shows two types of mixed or transitional flower types [26]. This is mainly due to the degradation or disappearance of most of the stamens, the partial petalization of stamens, and the hybridization of cultivars with different flower types, including natural hybridization and artificial hybridization.

To date, studies on the classification of tree peony flower types are quite scraggly. With the development of marketization, the flower industry is becoming more and more standardized. As various types of peony are common flower cultivars, standardized naming is particularly important and it requires the joint efforts of professional scholars.

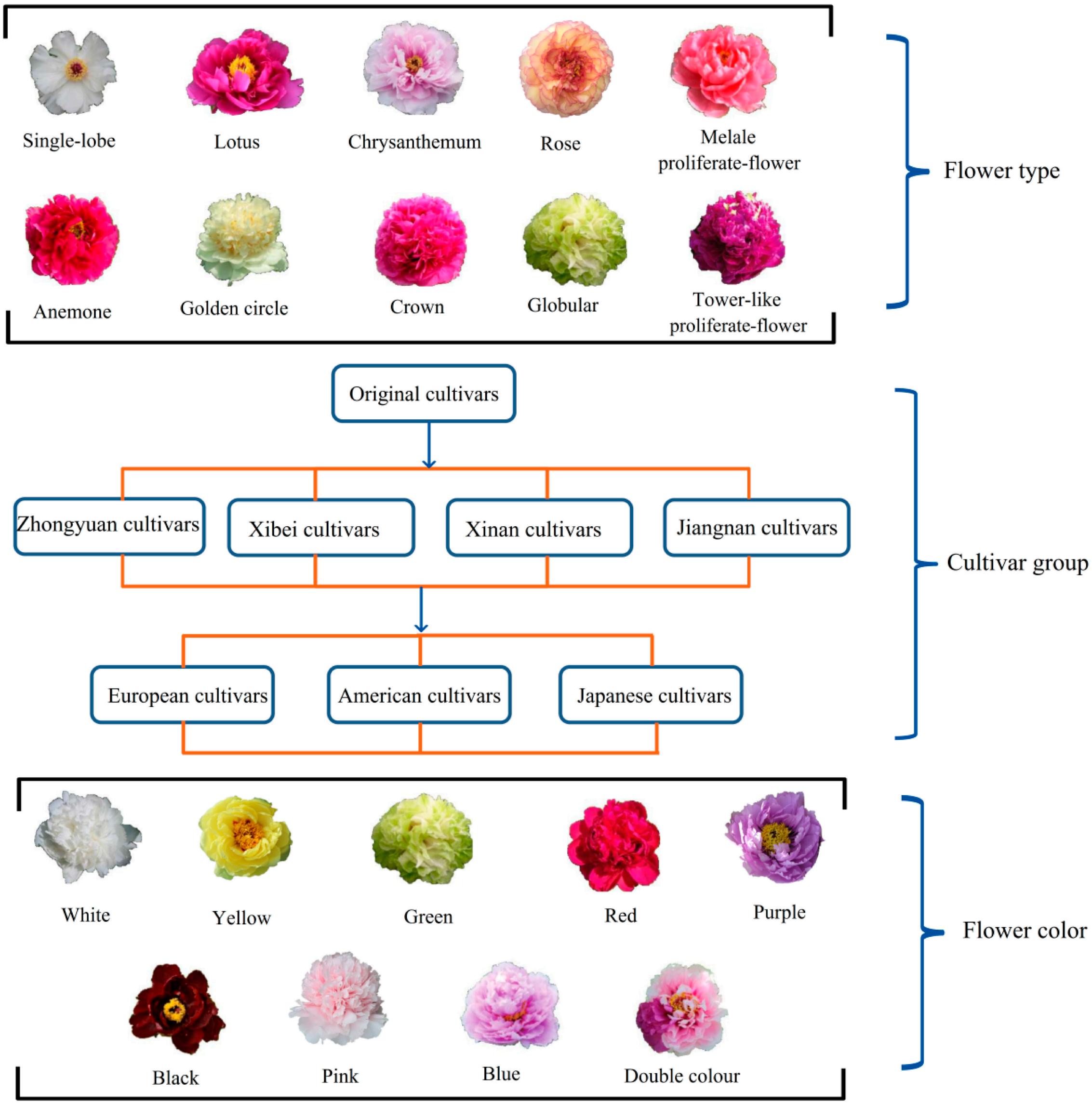

Figure 1. Schematic diagram of tree peony classification system.

Tree peony originated in China, mainly divided into four cultivars, and then developed into Japanese cultivars, European cultivars and American cultivars, respectively. The cultivated tree peony cultivars are classified into ten flower types and nine flower colors. Ten kinds of tree peony as a representative of the flower type: ‘Feng Dan’ (single-lobe type), ‘Si He Lian’ (lotus type), ‘Rou Fu Rong’ (rysanthemum type), ‘JinGe’ (rose type), ‘Cao Zhou Hong’ (melaleuca proliferate-flower type), ‘Greendragon sleeping pool’ (anemone type), ‘Yao Huang’ (golden circle type), ‘Shou An Hong’ (crown type), ‘Dou Lv’ (globular type) and ‘Guan Qun Fang’ (tower-like proliferate-flower type). Ten kinds of tree peony as a representative of the flower colour: ‘Jing Yu’ (white), ‘High Noon’ (yellow), ‘Dou Lv’ (green), ‘Zhao Yang Hong’ (red), ‘Wei Zi’ (purple), ‘Chu Wu’ (black), ‘Zhao Fen’ (pink), ‘Lan Fu Rog’ (blue) and ‘Er Qiao’ (double colour).

REGULATION MECHANISM OF FLOWER COLOR

Material Basis of Flower Color Formation

The formation of peony flower color depends on some basic substances, including carotenoids, anthocyanins and flavonoids [27]. Among these chemical constituents, carotenoids are important natural pigments and mainly affect the formation of peony red, orange, yellow and other flower colors [28]. In petals, carotenoids interact with other pigments to synergistically regulate flower color. The content of carotenoids in some yellow peony petals is higher, showing bright yellow, such as ‘Yao Huang’. In further research, the expression process of key structural genes controlling carotenoid content was basically consistent with the change trend of flower color in tree peony [29]. Apart from the yellow series, a small amount of carotenoids were detected from some of the purple peony cultivars, while the white and pink series did not contain carotenoids [30].

Anthocyanins are water-soluble plant pigments formed by the combination of cyanidins and sugars [4]. The types and contents of anthocyanins in peony show diversity due to different cultivars and development time, and are affected by environmental factors [13]. The red tree peony grown in acidic soil has a more red color. This may be because the PH value of the petal cell fluid directly affects the color performance of anthocyanins, resulting in differences in flower color. In most plants, anthocyanins give flowers and other organs pink, red, purple, and blue colors [31]. Except for ‘Fengdan’, white peony cultivars almost did not contain anthocyanin, and purple peony cultivars had higher anthocyanin content [32,33]. In the meantime, with the continuous accumulation of anthocyanin content, the content of flavonoids accumulated first and then degraded. With the opening of flowers, the anthocyanins and flavonoids in peony will be degraded to varying degrees, showing the change of flower color from red to yellow [32,34].

Flavonoids are the main factors influencing the color of petals, including glycosides and multiform glycosides of flavones and flavonols [23,26]. Existing studies have confirmed that flavonoids can produce a full spectrum of colors from pale yellow to bluish purple [35]. Recently, a total of 39 flavonoids were identified in 8 different color series from white to red, to yellow [36,37]. Compared with anthocyanins, flavonoids generally act as auxiliary pigments to regulate flower color. The content of total flavonoids in peony petals is consistent with the depth of flower color, that is, the more the total flavonoids content, the deeper the flower color, but for peony without anthocyanins, flavonoids will be the main compound affecting flower color [38,39]. The pigment composition of peony flower color is relatively complex, and different pigment content is the decisive factor for different flower color [38]. The anthocyanins of wild *Paeonia delavayi* in Yunnan are mainly flavonoids and chlorophyll, while flavonoids are mainly composed of a mixture of flavonoids, chalcone and flavonol [39]. In a recent study, flavonoids/flavonols and anthocyanins were confirmed to be the main contributors to petal coloring in ‘High Noon’ and ‘Rou Fu Rong’, respectively [39,40].

Molecular Mechanism of Flower Color Regulation

The bright and charming flower color of tree peony has received considerable attention. Benefit from the development of biotechnology and the related mechanism of peony flower color regulation has been well described and many genes involved in pigmentation have been reported [18]. The flower color of tree peony is mainly affected by carotenoids, anthocyanins and flavonoids [8,18]. A series of pigment metabolism processes related to it involve a variety of genes, including *PsCLH1*, *PsLhcb1/5*, *PsCHS*, *PsDFR* and *PsANS* [41–43]. The difference of peony flower color depends on the formation, transformation and accumulation of pigment products. Some transcription factors, especially R2R3-MYB, WD40 and bLHH family members, play important roles in regulating the expression of flavonoid biosynthetic genes and anthocyanin accumulation [44–46] (Figure 2).

The biosynthesis of flavonoids is regulated by many genes, including *ECHS*, *CHI*, *DFR* and *ANS* [10]. While, *PsF3H*, *PsDFR*, *PsMYB* and *PsWD40* are important factors regulating anthocyanin formation [46]. In a recent study, the two-color mechanism was analyzed in ‘Shima Nishiki’. In brief, *PsDFR* and *PsMYB* are positively correlated with anthocyanin concentration, while *PsWD40* is the opposite [39]. The differential expression of two genes (*PsF3’H* and *PsFLS*) was identified in ‘Er Qiao’, which caused the difference between safflower and white flower. The inhibition of *PsF3’H* protein content will lead to the inhibition of anthocyanin synthesis, resulting in the formation of ‘Er Qiao’ peony bicolor flowers [47,48]. In addition, the expression of some genes, such as *PsDFR*, *PsANS* and *PsUF3GT*, mediates the change of flower color by converting anthocyanidins into anthocyains [49]. Apart from the above factors, the genes that regulate pigment accumulation are also important factors for the formation of different flower colors, such as *PsF3H*, *PsDFR*, *PsANS*, and *Ps3GT* [8]. These four structural genes play an important role in purple pigmentation, and the high co-expression of *PsTHC2’GT*, *PsCHI*, and *PsFNS II* ensures the accumulation of yellow pigments in *Paeonia delavayi* wild population flowers [50]. In the petals of ‘Lv Mu Yin Yu’, *PsCLH1* reduced the chlorophyll content of the petals and promoted the chlorosis of the petals; *PsLhcb1* and *PsLhcb5* increased the chlorophyll content of petals and inhibited the chlorosis of petals [42].

In the regulation of flavonoid production, MYB is a key transcription factor that binds directly to the promoters of bHLH regulators or structural genes and is involved in activating gene expression. WD40, as a chaperone protein, is involved in the regulation of stable MBW complex

[51]. Other transcription factors, such as SPL, WRKY, HY5 and ERF, are also involved in the regulation of flavonoid biosynthesis. Among them, SPL can interfere with the formation of MBW complexes by competing for bHLHs or MYB, resulting in a decrease in anthocyanin accumulation [52–54]. Related studies have also reported the formation mechanism of pigmentation in tree peony. *PsMYB30* promotes the formation of pigmentation in 'High Noon', and *PsMYB12* promotes the formation of pigmentation in 'Qinghai Lake Yinbo' peony [40,49]. The structural gene excavated from 'High Noon' is *PsANS*, which is a downstream structural gene in the flavonoid biosynthesis pathway [49]. *PsMYB30* can regulate its gene expression; the structural gene excavated from 'Qinghai Lake Yinbo' peony is *PsCHS* gene, and its encoded product chalcone synthase is the first rate-limiting enzyme in the flavonoid biosynthesis pathway, which is regulated by *PsMYB12*. *PsbHLH* and *PsWD40* can interact with *PsMYB12* protein and act on the promoter of *PsCHS* gene. Silencing *PsMYB30* in peony petals will reduce and fade the color spots, and also reduce the content of anthocyanins and *Pn3G5G* [40]. This process is regulated by epigenetic modifications, such as DNA methylation. R2R3-MYB and bHLH transcriptionally activate EBGs and LBGs in a certain way, regulating the deposition of mottle pigments, while the hypermethylation of gene promoters in non-mottle regions leads to structural genes [40]. In addition, anthocyanins and flavonols are a competitive relationship in the process of peony petal coloration. A recent study described this mechanism, in which *MYBPA2* and *bHLH1-3* interact to activate the expression of F3H and promote the biosynthesis of anthocyanins, while *MYB21* regulates the accumulation of flavonols by activating the expression of *F3H* and *FLS* [55]. The high expression of *MYB21* inhibits the biosynthesis of anthocyanin. And *MYB308* inhibits the synthesis of anthocyanin, which depends on the interference of *DFR* and *MYBPA2* [55].

In recent years, deep sequencing of microRNA (miRNA) has been widely carried out in many plants and miRNAs are involved in various biological activities, including flower development, hormone signal transduction and stress response [56]. However, there are few reports on miRNA regulation of flower color. In herbaceous peony, 191 miRNAs showed differential transcription in red outer petals and yellow inner petals, and the regulation of miR156e-3p targeting *SPL1* contributed to the formation of yellow petals [57,58]. In tree peony, 'High Noon' and 'Rou Fu Rong' were also used to explore the potential mechanism of flower color regulation, and 9 differentially expressed miRNAs and 12 target genes related to flavonoid biosynthesis were identified. According to the expression profile of target genes and the accumulation pattern of flavonoids, it was speculated that *miR-138-PsCHI* module and *miR156b-PsSPL2* module may play a key role in the yellow pigmentation of 'High Noon' petals [41] (Table 1).

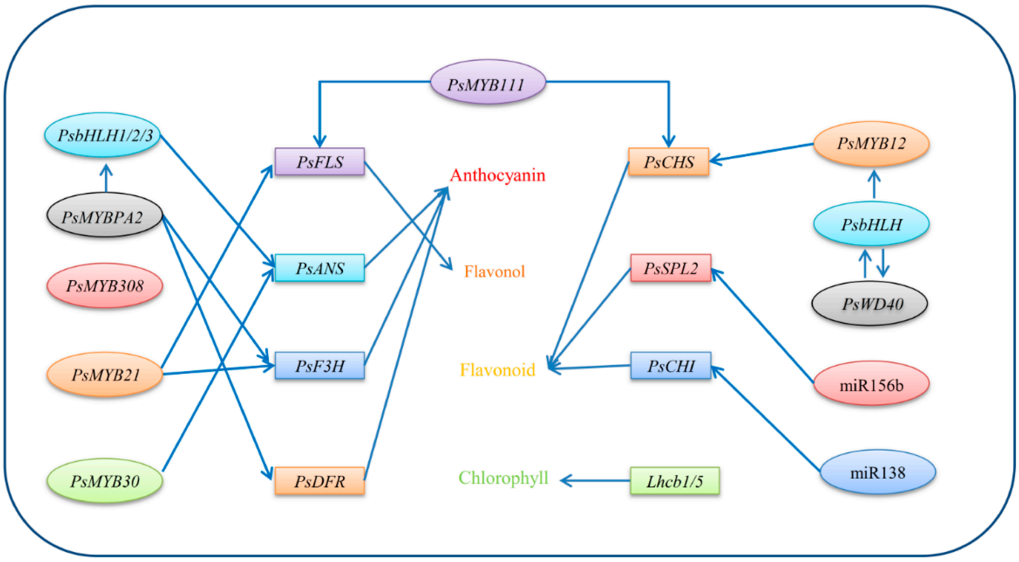

Figure 2. Molecular mechanism of pigment regulation in tree peony petals.

PsbHLH and *PsMYBPA2* form a complex, mediating *PsF3H*, *PsANS* and *PsDFR* to regulate anthocyanin accumulation. *PsMYB21* also regulates the expression of *PsF3H*. *PsMYB308* interferes with the expression of *PsMYBPA2* and *PsDFR*. *PsMYB21* and *PsMYB111* affected the synthesis of flavonols through *PsFLS*. *PsMYB12* also regulates *PsCHS* to affect flavonoid synthesis, and *PsbHLH* and *PsWD40* interact to mediate *PsMYB12* to regulate *PsCHS* expression. The *miR156b-PsSPL2* module and *miR138-PsCHI* module affected the accumulation of flavonoids. *PsLhcb1/5* contributes to chlorophyll synthesis.

Table 1. Summary of molecular regulation mechanism of flower color phenotype formation.

Cultivars	**Flower color**	**Regulator gene**	**Flower color regulation mechanism**	**Reference**
Paeonia ostii	Double color	*PoMYB2*, *PoSPL1*	*PoMYB2* and *PoSPL1* negatively regulate anthocyanin accumulation by affecting the activation ability of MYB-bHLH-WDR complex.	[41]
Lv Mu Yin Yu	Green	*PsCLH1*, *PsLhcb1*, *PsLhcb5*	*PsCLH1* reduced the chlorophy II content of petals and led to the chlorosis of petals; *PsLhcb1* and *PsLhcb5* increased the chlorophyll content of petals and inhibited the chlorosis of petals.	[42]
Qinghai Lake Yinbo	White	*PsMYB12*, *PsCHS*	*PsMYB12* interacts with basic bHLH and WD40 proteins in a regulatory complex that directly activates *PsCHS* expression.	[43]

Table 1. *Cont.*

Cultivars	Flower color	Regulator gene	Flower color regulation mechanism	Reference
Er Qiao	Double color	*PsF3'H*, *PsFLS*	Insertion and deletion of *PsF3'H* and up-regulation of *PsFLS* reduced anthocyanin content in petals.	[48]
Shima Nishiki	Red	*PsWD40*, *PsDFR*, *PsMYB*	*PsDFR* and *PsMYB* positively regulate the expression of anthocyanin, while *PsWD40* has the opposite effect.	[49]
Wild P. delavayi	Double color	*PsF3H*, *PsDFR*, *PsANS*, *Ps3GT*, *PsHC2'GT*, *PsCHI*, *PsFNS II*	*PsF3H*, *PsDFR*, *PsANS* and *Ps3GT* play an important role in the pigmentation of purple petals, while *PsHC2'GT*, *PsCHI* and *PsFNS II* regulate the accumulation of yellow pigments.	[50]
Cai Hui	Red	*PsDFR1*	*PsDFR1* regulates anthocyanin accumulation in petals.	[52]
High Noon	Yellow	*PsMYB30*, *PsANS*	*PsMYB30* can bind to the promoter of anthocyanin synthase (ANS) gene and enhance its expression to regulate anthocyanin accumulation.	[55]
Hong Yan Zheng Hui	Red	*PsDFR*, *PsANS*, *PsUF3GT*	*PsDFR*, *PsANS* and *PsUF3GT* are highly expressed during development and regulate anthocyanin accumulation.	[57]
Huang Jin Lun	Yellow	*PsCHI*	*PsCHI* negatively regulates the accumulation of chalcone and makes petals yellow.	[57]

REGULATION OF FLOWER TYPE

Field Factors Affecting Peony Flower Type

In the actual cultivation and production, most cultivars are mainly single flower type, but some cultivars have multiple flower types [8]. Different flower types can also be presented on the same plant, or the same plant can produce different flower types in different years or even different regions [59]. Therefore, the field performance of peony flower type is relatively stable and unstable. Among them, the flower types of the 'Shou An Hong' and 'Lv Mu Yin Yu' in the Chinese Zhongyuan cultivars are basically consistent and stable in different regions or under different environmental conditions [8,42].

Moreover, the flower types of some tree peony cultivars are different from the original cultivars. In different years, they will develop from lotus type to crown type, and may open different flower types in two different regions, which is also called flower type instability [60]. Interestingly, some tree peony cultivars have multiple flower types such as single petal type, lotus type and crown type at the same time on the same plant, such as ‘Zhao Fen’, and there are obvious ‘on-year and off-year’ phenomenon. The flower type is rich in crown type in on-year, and the flower type is mostly lotus type, single petal type or laurel type in off-year [8,61]. In last decades, several studies have made some explanations for the regulatory mechanism. Cold stress inhibits the development of flower buds and causes malformed flowers. This may be due to hormone and carbohydrate biosynthesis is affected, especially GA_3 [62,63]. Under waterlogging, the photosynthesis of tree peony is blocked, the reduction of nutrients and the change of hormone level lead to irregular and distorted petals [64,65]. Furthermore, light, plant growth regulators, fertilizers, and diseases are also potential candidates for regulating flower shape changes, but the existing research related to it is very limited.

Thus, environmental factors are important factors affecting the formation of peony flower patterns and there is a certain relationship between the degree of double petals of peony flowers and the environment, cultivation conditions and nutrient supply differences between branches [31]. Extreme weather conditions and poor cultivation management can lead to changes in tree peony flower type [66,67]. However, environmental factors including light, temperature, water, plant growth regulators, fertilizer, drought, disease and other factors on the specific collaborative regulation of the impact of flower type is unclear.

Molecular Mechanism of Flower Type Regulation

The increase of petals and petalization of stamens caused by artificial selection innovation are the main reasons for the change of peony flower type [25]. In last decades, the researches of domestic and foreign scholars on the regulation mechanism of peony flower type mainly focuses on the typical flower development model genes [68]. These genes are involved in a series of regulations including the morphology, quantity, variation and arrangement of petals, stamens, pistils and sepals (Figure 3). In peony, the MADS-box gene family is an important factor in regulating flower development of tree peony [17]. Many members have been described, including *PsAP1*, *PsPI*, *PsMADS1*, *PsMADS9*, *PsAG* and *PsMADS5* [9,18].

PsMADS5, *PsMADS7* and *PsMADS12* can regulate the differentiation of pistil and stamen primordium, the development of calyx and petal, and participate in the stamen petalization of flower types [18]. In ‘Luo Yang

Hong', *PsAGL6* is involved in the formation of peony petal organs, and *PsAGL6*, *PsAP2* and *PsEDA3* are likely to be involved in the development of peony flower type by regulating the key genes of peony stamen petalization [69]. The MADS-box family genes related to floral organ development in *P.lactiflora* were identified, and the expression of *PsAP1*, *PsAP2* and *PsSEP3* was also increased, while the expression of *PsAP3-1*, *PsAP3-2* and *PsPI* was opposite during the increase of the degree of petals. Further studies showed that *PsAP1* and *PsSEP3* mainly regulated sepals and petals, while *PsAP3-1*, *PsAP3-2* and *PsPI* mainly regulated stamens and petals [70,71]. In another study of 'Luo Yang Hong', *PsAP150* gene may be involved in the regulation of sepal primordium and bract primordium differentiation. *PsAP185* gene may be involved in the formation of peony petals and regulate the differentiation of sepal primordium of single-petal peony. *PsPI72*, *PsAP353*, *PsAG69*, *PsSEP1* and *PsAP353* are involved in the regulation of the formation and development of petals, stamen primordia, pistils, sepals and stamen petalization, respectively [72–74] (Table 2).

In the long-term evolution process, the flower types of tree peony are gradually diversified and complicated due to the extensive homoploid hybridization involved in the domestication process of tree peony [18,75,76]. The application of molecular technology has been greatly helpful to the study of the mechanism of tree peony flower development. According to the ABCDE model, it is an effective method to speculate the main mechanism of peony flower type diversity [9,18]. Further research is needed to explore the molecular regulation relationship between different flower types of tree peony.

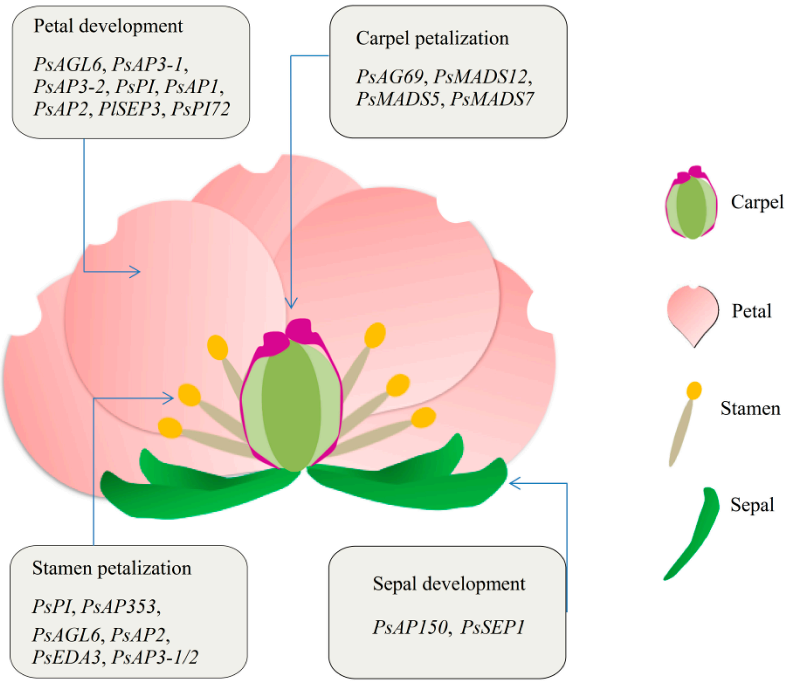

Figure 3. Genes in the regulation mechanism of flower type.

The genes involved in the regulation of petal include *PsAGL6*, *PsAP3-1*, *PsAP3-2*, *PsPI*, *PsAP1*, *PsAP2*, *PsSEP3*, *PsPI72*; *PsAG69*, *PsMADS12*, *PsMADS5* and *PsMADS7* are involved in the regulation of pistil; *PsAP150* and *PsSEP1* regulate sepal development. The genes regulating stamen petalization are *PsPI*, *PsAP353*, *PsAGL65*, *PsAP2*, *PsEDA3*, *PsAP3-1* and *PsAP3-2*.

Table 2. Summary of molecular regulation mechanism of flower type phenotype formation.

Cultivars	Flower type	Regulator gene	Flower type regulation mechanism	Reference
Luo Yang Hong	Rose type	*PsAGL6*	*PsAGL6* is highly expressed in sepals, stamens and petals and may be involved in the regulation of petal formation in flowers.	[69]
Zhao Fen	Golden circle	*PsAG*	*PsAG* is highly expressed during flower development and is involved in regulating flower development.	[70]
Feng Dan	Single-lobe type	*PsAP2*	*PsAP2* is up-regulated in flower development and is involved in the regulation of flower development.	[71]
Luo Yang Hong	Rose type	*PsAP150*, *PsAP185*	*PsAP150* regulates the differentiation of sepal primordium and bract primordium, and *PsAP185* may regulate the formation of peony petals.	[72]
Er Qiao	Rose type	*PsAP1*, *PsAP2*	*PsAP1* and *PsAP2* are involved in the regulation of organ identity determination in petals and petalized stamens.	[73]
Luo Yang Hong	Rose type	*PsPI*	*PsPI* is involved in the differentiation of pistil and stamen primordium, and regulates the process of pistil and stamen petalization.	[74]

CONCLUSION AND FUTURE PROSPECTS

In this review, the development regulation mechanisms of two major traits of flower type and flower color in tree peony in recent years are summarized. Functional genes related to flavonoids, anthocyanins and carotenoids are the main regulators affecting flower color. And the changes in the concentration of these compounds in the petals directly mediate the color change. In the regulation mechanism of tree peony flower type, it mainly focuses on the mining and verification of typical flower model genes [8,18]. Compared with model plants, the study of these mechanisms is still very simple, especially the lack of a stable genetic transformation system, resulting in the limitations of functional verification of these genes.

In view of the complexity of the development and evolution of tree peony, future research can focus on the following aspects. First, pay attention to the study of more tree peony cultivars, especially those with representative flower characteristics of the cultivars, should be developed into a model. Theoretically, the use of new techniques to study these typical cultivars not only contributes to the study of tree peony development, but also contributes to the test of the hypothesis derived from comparative analysis. Secondly, attention should be paid to the application of advanced technologies, not only multi-omics technology, but also machine learning and computer modeling, which should be integrated into the classical genetic regulation mechanism, especially the study of different flower colors and patterns among the same cultivars. In addition, the whole regulatory network of flower development can be studied from the process and mode of evolution, rather than a single functional gene [77,78]. Many functional genes and transcription factors have been discovered and applied to the study of peony. It is necessary to establish a stable genetic transformation system of peony as soon as possible, introduce functional genes of target traits, and carry out directional breeding.

DATA AVAILABILITY

Data will be provided on reasonable request.

AUTHOR CONTRIBUTIONS

Writing-Original Draft Preparation, DDZ; Writing-Review & Editing, DLG and XGH; Funding Acquisition, XGH.

CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

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